

MOLT PATTERNS AND MOLTING GROUNDS OF LUCY'S AND VIRGINIA'S WARBLERS: SIMILAR YET DIFFERENT

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ABSTRACT.—Using museum specimens, we documented the molt cycles and molting grounds of adult Lucy's (*Vermivora luciae*) and Virginia's (*V. virginiae*) warblers. During prebasic molts, both species replace all body plumage. Prebasic primary molt takes a mean of 71 days for Lucy's Warblers, but a mean of just 42 days for Virginia's Warblers. Prebasic molt occurs exclusively on the breeding grounds. We found no evidence of a prealternate molt in Lucy's Warblers, and limited evidence of a prealternate molt in Virginia's Warblers. In both species, the seasonal change in crown color is a function of the freshly replaced gray-tipped feathers acquired during the prebasic molt being abraded during the winter, such that the basal red coloration of those same feathers is exposed during spring. These species differ from other western-breeding passerines in that they do not appear to directly exploit the late season food resources in the southwestern United States and northwestern Mexico. This difference is suggested by the lack of a shift from northern parts of their breeding range to molt in those potentially more productive regions of the southwestern monsoon region. The possibility of winter territoriality may play a role in the rapid prebasic molt exhibited by Virginia's Warblers. On the other hand, the lengthy prebasic molt of Lucy's Warblers may be explained by the use of poor nutritional resources during late summer, and/or the lack of territoriality during late summer and winter. We conclude that our data, in conjunction with data from previous studies, suggest multiple contrasting molt migration strategies among breeding passerines in western North America. Received 4 September 2001, accepted 2 June 2002.

Molt studies of birds which breed primarily in the western portions of North America have suggested interesting life history trade offs. The most widespread of these patterns is molt migration, which has been found in a number of diverse lineages (Rohwer and Manning 1990, Young 1991, Voelker and Rohwer 1998). Molt migration involves commencing the fall migration prior to the fall (prebasic) molt. This fall migration is then interrupted, as birds stop in the Sonoran and Chihuahuan desert regions of the southwestern United States and northwestern Mexico to begin molting. A stopover in this region allows molt-migrating species to avoid the late season droughts and corresponding loss of food availability on their breeding grounds, and to take advantage of food flushes produced in southwestern desert areas by late summer monsoon rains (Baldwin 1973, Rohwer and Manning 1990, Voelker and Rohwer 1998). The late summer monsoon region includes southeastern Colorado, eastern Arizona, New Mexico, the western extremes of Texas, the

eastern two-thirds of Sonora, and all of Chihuahua, and extends southward into Mexico to at least 20° north latitude (Comrie and Glenn 1998).

This pattern of molt migration raises an interesting question: do birds that breed in the xeric western and southwestern portions of the United States, but winter farther south, also take advantage of the late summer increase in resource availability? If so, such western- and southwestern-breeding species should be concentrated in the molt migration area during some or all of their fall molting period. Evidence of such a pattern would be molting birds in species with disjunct breeding and wintering ranges that do not include the Mexican monsoon region being found predominantly in the molt migration area during their molts. Further, molting birds in species whose breeding or wintering ranges include portions of the Mexican monsoon region also should be concentrated in the monsoon region during molt.

This question was addressed initially by a study of molt in the Gray Vireo (*Vireo vicinior*; Voelker 2000). That study suggested that Gray Vireos do not take advantage of late summer resources by concentrating to molt in the molt migration stopover areas, and that they require a mean of 10 days longer to molt than do molt-migrating species. These results

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suggest the possibility that not only do molt-migrating species make use of desert food flushes, but that they also may be able to molt faster as a consequence.

In this paper we explore further the question of whether western- and southwestern-breeding species take advantage of late summer resource availability in molt migration areas by documenting the molting areas of Lucy's (*Vermivora luciae*) and Virginia's (*V. virginiae*) warblers. Both of these species breed throughout the western and southwestern United States, including portions of the molt migration area, and winter farther south along the western coast of Mexico. We also describe in detail the annual molt cycle of both species, including the seasonal color changes exhibited by *Vermivora* warblers.

METHODS

Study species.—Lucy's Warblers breed through southeastern California and along the southern third of the California-Nevada border, extreme southern Nevada, southern Utah, extreme southwestern Colorado, extreme northwestern New Mexico, north, west, and south Arizona excluding the extreme southwest, to southwestern New Mexico, the southwestern edge of Texas, extreme north and northeastern Chihuahua, northeastern Sonora, and extreme northeastern Baja California (Johnson et al. 1997, American Ornithologists' Union 1998). Breeding occurs most often in dense riparian mesquite (*Prosopis* spp.) woodlands, but habitats dominated by tamarisk (*Tamarix* spp.) also are used (Johnson et al. 1997). Lucy's Warblers winter from southern Sonora south to Oaxaca in a narrow strip along the Pacific coast and adjacent inlands, and sometimes along the central portion of the Texas-Chihuahua border (Johnson et al. 1997, American Ornithologists' Union 1998). Wintering habitat typically is restricted to dry washes, riparian gallery forests, and thorn scrub (Johnson et al. 1997). Winter territoriality has not been observed in these birds, and they are known to occur in mixed species flocks (Johnson et al. 1997). That portion of their breeding range which includes southeastern Arizona, southwestern New Mexico and Texas, and Chihuahua and Sonora is within the primary monsoon, or molt migration area, as are both the migratory range and the northern half of their wintering range (see Johnson et al. 1997, Comrie and Glenn 1998).

Virginia's Warblers breed throughout extreme southeastern California, Nevada excluding the northwest, southeastern Idaho, southern Wyoming, western South Dakota, Utah, Colorado excluding the east, Arizona except in the southwest and extreme west, New Mexico excluding the east, and into part of southwestern Texas. Breeding habitat includes pinon-juniper (*Pinus* spp. and *Juniperus* spp.) and oak (*Quercus* spp.) wood-

lands, dense mountain mahogany (*Cercocarpus* spp.), and brushy cover along streamsides (Olson and Martin 1999). Late in the breeding season Virginia's Warblers often are observed moving into low foothills (Phillips et al. 1964, Bailey and Niedrach 1965), and during migration they may depend strongly upon riparian corridors, where they often join mixed species flocks (Olson and Martin 1999). The winter range of Virginia's Warblers is from southern Nayarit and northern Jalisco south to southern Puebla and central Oaxaca (American Ornithologists' Union 1998, Olson and Martin 1999). Wintering habitat includes thorn scrub, and tropical deciduous, oak, and pine-oak woodlands (Olson and Martin 1999). Winter territoriality has not been reported. That portion of their breeding range which includes eastern Arizona, southeastern Colorado, New Mexico, and Texas is within the late summer monsoon region, as are both the migratory range and the northernmost portion of their wintering range (see Comrie and Glenn 1998, Olson and Martin 1999).

Scoring molt.—We examined 334 adult specimens of Lucy's and 287 adult specimens of Virginia's warblers from 28 museum collections (see acknowledgments). We used data from museum labels to determine gender, collection date, and collection locality of each specimen, and we used data from museum labels or plumage characters (see Pyle et al. 1997) to exclude hatching year birds from the analyses. We examined specimens under a 3× magnifying lamp lighted with a 22-watt fluorescent bulb, using a small forceps to lift feathers and quantify molt. We scored body molt by estimating the percentage of feathers growing in each of five regions: chin and throat, breast, belly, head, and back (definitions in Rohwer 1986). Percentage categories were 0, 10, 30, 50, 70, and 90% of feathers developing (Rohwer 1986). We summed the scores from the five regions and calculated a mean overall body molt score.

Both species have nine primaries and secondaries on each wing and 12 rectrices. To score flight feather molt, we followed Rohwer (1986) in estimating the fraction of the full length (by 0.1 intervals) each developing feather had reached, and scored missing feathers as 0. We used N to designate newly replaced feathers, and X to designate feathers not yet replaced on molting specimens (Voelker and Rohwer 1998). A hypothetical data sheet for a specimen replacing primaries on one wing reads: N, N, N, 0.9, 0.7, 0.3, 0, X, X, where primaries 1–3 are newly replaced and fully grown, primaries 4–6 are growing feathers, primary 7 is missing, and primaries 8–9 have yet to be dropped. The molt score for this wing is 4.9, where each N is scored as 1. Both wings of each specimen were examined and scored.

We generally followed Rohwer (1986) to determine whether molt was adventitious. However, we did score asymmetrical primary feather molt if one or more contiguous feathers were missing on one wing and not the other as long as the primary one was included in the missing feathers. We did this because primary molt often is not synchronized in these two species, with

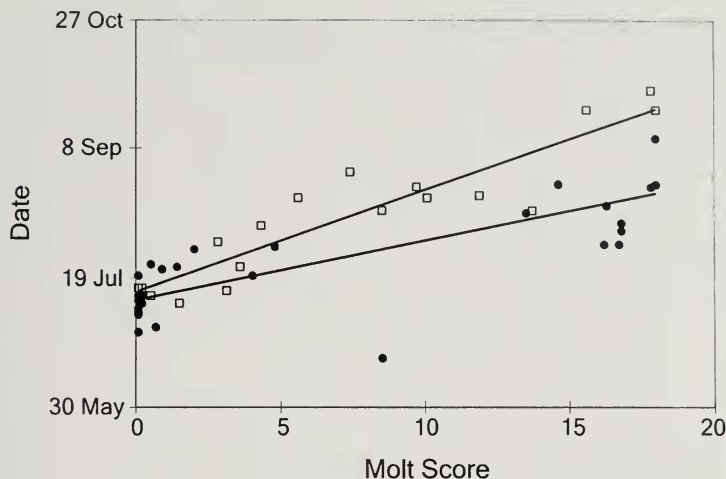


FIG. 1. Regression of collection date (Julian) over primary molt score, to estimate the time necessary to complete prebasic molt. Lucy's Warblers (*Vermivora luciae*; open squares) required a mean of 71 days to complete the prebasic molt ($y = 194.4 [= 13 \text{ July}] + 3.97X$, $r^2 = 0.85$, $n = 19$, $P < 0.001$), while Virginia's Warblers (*V. virginiae*; filled circles) required a mean of only 42 days ($y = 191.3 [= 10 \text{ July}] + 2.29X$, $r^2 = 0.66$; $n = 29$; $P < 0.001$). Data are from museum skins. See text for calculation of primary molt scores.

one wing beginning to molt slightly before the other (Voelker 2000).

We estimated the rate and duration of primary feather molt using Pimm's (1976) regression method, with date of collection (in Julian days) as the dependent variable and the summed score of growing and newly replaced primary feathers as the independent variable. The y intercept from the regression represents the mean molt initiation date. We calculated the mean molt completion date by replacing the x value from the regression equation with the maximum molt score value (here, 18), and solving Julian date. This method provides a mean estimate of primary molt duration for all individuals, and thus is more appropriate than reversing the axes, which is valid only when a single bird is followed through time (Pimm 1976, Langston and Rohwer 1996). Although all regression models for estimating molt are necessarily imperfect (Voelker 2000), Pimm's method is less so because it overcomes the problem of heteroscedasticity in molt data. All specimens that were molting primaries were included in the regression analyses.

We followed the molt terminology of Humphrey and Parkes (1959), and followed Langston and Rohwer (1996) in determining molt series (see Yuri and Rohrer 1997 for a detailed explanation of patterns of feather replacement and identification of molt series). Briefly, based on its stage of growth and the stage of growth of adjacent feathers, each developing feather can be categorized as nodal, terminal, or directional. Nodal feathers are replaced first in a series and are always closer to full length than adjacent feathers. Terminal feathers are replaced last in a series and are always less fully grown than adjacent feathers. The lengths of other developing feathers indicate whether the direc-

tion of feather replacement within a series proceeds proximally to distally, or distally to proximally.

RESULTS

Definitive prebasic molt.—Lucy's Warblers underwent prebasic molt from July through September (Fig. 1). Of the 36 specimens we examined from this period, 19 were molting. Virginia's Warblers were molting from June through September (Fig. 1). Of the 116 specimens we examined from this period, 29 were molting. All feathers in both species are replaced during the definitive prebasic molt; the primaries are replaced proximally to distally in a single series, beginning with P1 and ending with P9 (Table 1). P1 is always nodal, and was the only nodal feather for seven specimens of Lucy's Warblers and 14 specimens of Virginia's Warblers. However, four specimens of Lucy's Warblers and four specimens of Virginia's Warblers demonstrated that P2 also can be nodal, being dropped at the same time as P1 (Table 1). One specimen of Lucy's Warbler had dropped P1, P2, and P3 simultaneously. For three specimens of Lucy's Warblers and 12 specimens of Virginia's Warblers, P9 was the only terminal primary; one specimen of Virginia's Warbler had two terminal feathers, P9 and P8 (Table 1). The regression of collection date on primary molt score suggests

TABLE 1. Patterns of flight feather replacement in molting Lucy's (*Vermivora luciae*) and Virginia's (*V. virginiae*) warblers. Numbers in each column refer to the number of specimens in which each focal feather was being replaced. Nodal feathers are lost first in a molt series and indicate molt series initiation points, while terminal feathers are replaced last and indicate molt series completion points. Other growing feathers indicate directionality, which is determined by the condition of adjacent feathers relative to each focal feather. For both species, primary molt was initiated at primaries 1–3, proceeded proximally to distally (where each focal feather was not as far along in molt as the next most proximal feather, but farther along in molt than the next most distal feather) and terminated at primary 9. Secondaries were replaced in three or four series, as indicated by nodal feathers. Rectrices were replaced in one series. Data are from museum skins.

Molt patterns	Focal feather																							
	S9	S8	S7	S6	S5	S4	S3	S2	S1	P1	P2	P3	P4	P5	P6	P7	P8	P9	R1	R2	R3	R4	R5	R6
Lucy's Warbler (<i>n</i> = 18)																								
Proximal to distal molt			1					1			3	5	4	6	5	3	3				3	2	2	2
Distal to proximal molt		1			2	2	2	1																
Nodal feathers		5	1	2				4	7	4	1								4					
Terminal feathers	3		1	2														3					1	4
Virginia's Warbler (<i>n</i> = 29)																								
Proximal to distal molt					2	7	5	4			6	3	3	3	1	6	8					1	1	1
Distal to proximal molt																								
Nodal feathers		3		6				2	14	4									3					
Terminal feathers	1		1	7	10	2											1	12						4

primary replacement lasts a mean of 71 days in Lucy's Warblers, and 42 days in Virginia's Warblers (Fig. 1).

Secondary feathers are replaced in two, or possibly three, series for both species: S1 to S6 and S7 to S9, or S1 to S5, S6, and S7 to S9. The inner series is started first, at about the same time that P3 to P5 are being replaced. S8 generally is the nodal feather in this series (Table 1). However, one Lucy's Warbler had S7 as the nodal feather while S8 was scored as distal to proximal. S7 also was replaced after S8 but before S9, or at about the same time as S9. S9 always was terminal.

The outer secondary series is replaced distally to proximally (Table 1), with nodal feather S1 dropped at about the same time as P5 to P6. In all cases, S5 appears to be part of an S1 to S5 series. Therefore, S5 may in fact be the terminal feather of the distal secondary series. In one specimen of Virginia's Warbler, S4 also was a terminal feather. This distal secondary series generally is completed when the primary series is complete or shortly thereafter.

S6 may constitute its own molt series. In all cases where S6 was being replaced, S7 to S9 were fully grown, suggesting that S6 is not a part of that series. In 2 of 4 Lucy's Warblers and 6 of 13 Virginia's Warblers where both S6 and S5 were being replaced, S6 was more fully grown than S5, indicating that S6 was dropped first. Thus, S6 may not be part of the S1 to S5 series, at least in some individuals.

Rectrix molt begins about the time that P2 or P3 is dropped, and in both species is finished before primary feather molt is completed. In most specimens molting rectrices, feathers were replaced in a single series, with R1 as the nodal feather and R6 as the terminal feather. However, in 4 of 14 Lucy's Warblers and 3 of 12 Virginia's Warblers several rectrices were dropped at very nearly the same time, and in no apparent order (these seven specimens were not scored in Table 1).

Body molt overlaps primary molt in both species. In Virginia's Warblers, all five body regions appear to be molting by the time P2 to P3 are being replaced. All five regions are molting when P1 is replaced in Lucy's Warblers; therefore, body molt in Lucy's Warblers may begin slightly earlier.

Definitive prealternate molt.—We found

just 9 of 84 specimens of Virginia's Warblers and 1 of 218 Lucy's Warblers collected between 1 January and 30 April to be molting. All nine specimens of Virginia's Warblers were molting body feathers, just six were replacing head feathers, and none were replacing flight feathers. This appeared to be a light body molt; only one specimen was molting in all five body regions and the highest overall body molt score was 24%. The single molting specimen of Lucy's Warbler was replacing body feathers on the chin and throat, and head regions (overall molt score of 12%).

Molt in relation to migration.—Every molting specimen of both species had been collected on the breeding grounds, and molting specimens were distributed throughout their breeding ranges. Further, we did not find birds in worn plumage on wintering grounds or in the migratory range during periods immediately following breeding. This strongly suggests that both species complete the prebasic molt on the breeding grounds before migrating to the wintering grounds, and that they are not making use of the southwestern monsoon region for molt.

DISCUSSION

Molt patterns.—Both Virginia's and Lucy's warblers replace their primaries in the pattern typical of most passerine species studied thus far. Several specimens from both species had S6 longer than S5 when both of these feathers were being replaced simultaneously. This pattern suggests that S6 is not a part of a single S1 to S6 series, but instead constitutes its own series. This pattern also is found in the Orange-crowned Warbler (*Vermivora celata*; Foster 1967), as well as in a number of New and Old world species from other genera (Jenni and Winkler 1994, Voelker 2000).

Rectrices in both species appear to be dropped in a single series, R1 to R6, and usually very rapidly. Four specimens of Lucy's Warblers and one specimen of Virginia's Warbler suggest that on occasion, rectrices are dropped so close in time that no pattern of replacement is apparent. This very rapid, nearly simultaneous loss of rectrices also has been documented in the Orange-crowned Warbler (Foster 1967). There is no evidence that R6 constitutes a molt series separate from R1 to R5, as has been documented in other recently

studied passerine species (e.g., Jenni and Winkler 1994, Voelker and Rohwer 1998, Voelker 2000).

We found no evidence of a prealternate molt in Lucy's or Virginia's warblers, yet both possess red crown patches which are evident to various extents during spring. Crown feathers acquired during the prebasic molt are mostly red, but have gray tips that mostly conceal the underlying red, and thus the crown patch. Therefore, the red crown patches apparent in these species during spring are the result of feather wear, in which the gray tips of these feathers wear away. This pattern of crown color change due to feather wear, suggested by Johnson et al. (1997) for Lucy's Warblers, also is evident in the Colima Warbler (*Vermivora crissalis*; Beason and Wauer 1998), and most likely occurs in the Orange-crowned Warbler as well (Foster 1967). As in Lucy's and Virginia's warblers, there appear to be a few individuals of Orange-crowned Warblers that undergo a prealternate molt (Foster 1967). Although quantitative data are lacking, the eastern race of the Nashville Warbler (*V. ruficapilla*) is presumed to replace head feathers during a prealternate molt, but with little resulting change in appearance (Curson et al. 1994). Because the newly replaced crown feathers in Nashville Warblers do in fact have gray tips which largely conceal the underlying red portion of the feathers, it is probable that red crown patches in this species also are the result of feather tip wear rather than feather replacement.

Timing of molt and migration.—Lucy's Warblers and Virginia's Warblers undergo the prebasic molt on the breeding grounds, as do almost all other *Vermivora* species (the *sordida* race of the Orange-crowned Warbler is the only known exception; Foster 1967, Curson et al. 1994, Beason and Wauer 1998).

Neither Lucy's nor Virginia's warblers perform a molt migration, i.e., they do not travel to a nonbreeding, nonwintering area to molt. They also do not concentrate in those portions of their breeding ranges which fall within the southwestern monsoon region. Performing molt migration is hypothesized to allow western North American species that breed in arid or in dry riparian habitats to take advantage of food flushes associated with late summer monsoons in southwestern United States and

northwestern Mexican deserts (Szarek 1979, Nielson 1986). To date, four western species have been shown to perform such a molt migration (Bullock's Oriole, *Icterus bullockii*, Rohwer and Manning 1990; Western Painted Bunting, *Passerina ciris pallidior*, Thompson 1991; Lazuli Bunting *P. amoena*, Young 1991; and Western Warbling Vireo, *Vireo gilvus swainsonii*, Voelker and Rohwer 1998), and one species has been shown not perform it (Gray Vireo, Voelker 2000).

We had predicted that both Lucy's and Virginia's warblers would be taking advantage of late summer food flushes associated with monsoons in the southwestern United States and northwestern Mexico. This would be accomplished by moving away from northern and western portions of their breeding ranges, which presumably have lower resource availability during late summer. This presumption is due to the paucity of late summer rains in the northern and western portions of the breeding range of each species, compared to the rains associated with the monsoon region (Comrie and Glenn 1998). Therefore, we had expected to find one of two patterns. First, that molting specimens would be concentrated in the southern and southwestern portions of their range, as Bullock's Oriole has been shown to do (Rohwer and Manning 1990). The second possible pattern was that most molting specimens would have been collected outside of their breeding range, including the wintering grounds. This pattern was found in Painted Buntings (Thompson 1991). Either of these patterns would have suggested that these species were performing molt migration, and thus were likely taking advantage of late summer desert food flushes. Clearly, neither of these patterns is evident in Lucy's and Virginia's warblers, nor was either pattern evident in Gray Vireos, which breed in similar xeric regions of the United States (Voelker 2000).

There are several possibilities to explain why Lucy's and Virginia's warblers do not migrate away from their breeding grounds prior to molting. One is that they have sufficient resources for molt on their breeding grounds, making a molt migration unnecessary. This possibility was used to explain why the western-breeding Hermit (*Dendroica occidentalis*) and Townsend's (*D. townsendi*) warblers, which breed in more productive habitats, do

not perform a molt migration (Jackson et al. 1992).

Another possibility is that, given the relatively short distance between breeding and wintering ranges, these two species have sufficient time between breeding and migration to complete the prebasic molt. By comparison, species which migrate farther (such as molt migration species) may be forced by time constraints to molt someplace other than on the breeding grounds. Such time constraint arguments have been widely applied (Jenni and Winkler 1994), but generally overlook species or group specific patterns due to a lack of ecological comparisons between breeding and wintering ranges (Voelker 2000).

Indeed, such a "sufficient post breeding time" time constraint hypothesis is not a satisfying explanation for the observed molt duration differences between Lucy's and Virginia's warblers. Lucy's Warblers require a mean of 71 days to complete molt while Virginia's Warblers take just 42 days (Fig. 1). If this disparity was due to differences in breeding duration or breeding times, a difference would be expected in the mean molt initiation dates for the prebasic molt. However, the mean molt initiation dates are very similar for the two species, with most individuals of both species beginning to molt in mid-July. The difference lies in the mean molt completion dates, with Lucy's Warblers completing molt in late September, and Virginia's Warblers in late August (Fig. 1). This difference strongly suggests ecological or behavioral differences either in late summer on the breeding grounds, or on the wintering grounds, and thus potentially different constraints.

With respect to Lucy's Warblers, molt duration may be explained by wintering ecology and behavior. During winter, this species tends to form small flocks and occupy a habitat similar to that occupied on the breeding grounds (Johnson et al. 1997). Therefore, a lack of winter territoriality, and similarity of breeding and wintering habitats (and therefore potential similarity of food resources), could explain the comparatively prolonged molt period in this species; there may be no advantage of an increased molt rate. This explanation is different from that offered for the prolonged molt of Gray Vireos (Voelker 2000), which was attributed to the defense of winter territories and

the associated late availability of winter food resources.

Notably, the mean length of molt for Lucy's Warblers is very similar to that of Gray Vireos (71 and 67 days, respectively), and the molt duration in these two species, neither of which is constrained to molt rapidly, is somewhat longer than the molt duration of species shown to perform a molt migration (54–57 days; Thompson 1991, Young 1991, Voelker and Rohwer 1998). This supports the hypothesis that molt-migrating species may be able to increase the rate at which the prebasic molt can be accomplished by making use of abundant resources (Voelker 2000). Further support of this idea is reflected in the seasonal diet of Lucy's Warblers, which switch to abundant but nutritionally poor food resources (leafhoppers) in July (i.e., when molt commences) after breeding is completed (Johnson et al. 1997). This suggests that the nutritional value of food is likely a key to the ability to molt more rapidly; it already is well documented that nutrition plays an important role in molt efficiency (Murphy and King 1992, Murphy and Taruscio 1995).

The short molt duration in Virginia's Warblers is more difficult to explain, largely because there is little information on its diet and wintering ecology (Olson and Martin 1999). One explanation might be that the difference in molt duration, compared to that of Lucy's Warblers, is due to a difference in the timing of migration. However, for migration timing differences to be a valid explanation in this case, Virginia's Warblers should depart the breeding grounds first. Instead, the opposite is true; Lucy's Warblers begin to leave the breeding grounds a full month before Virginia's Warblers (Johnson et al. 1997, Olson and Martin 1999).

Alternatively, Virginia's Warblers are difficult to detect on the breeding grounds by late July; it has been suggested that they disperse to lower elevations (and thus to potentially different habitats) before the onset of migration, which peaks in August (Phillips et al. 1964, Bailey and Niedrach 1965). Thus it is possible that breeding habitats have low resource availability during late summer, and that Virginia's Warblers may be changing to more productive habitat associations, such as riparian corridors (albeit still within the limits

of the geographic breeding range) during the molt period. Therefore, the comparatively rapid molt in this species may be attributable to the availability of abundant, late season, high nutrition resources within the breeding range.

The possibility of winter territoriality or winter food resource defense in Virginia's Warblers should not be ruled out as causal factors of a rapid molt. The need to establish and maintain winter territories certainly could drive the evolution of a very rapid molt. That this molt occurs on the breeding grounds suggests the possibility that resources on such a wintering territory may not be abundant enough, or may not be of sufficient nutritional value to support regular daily maintenance, the costs associated with replacing feathers, and the costs of territorial defense, as has been argued elsewhere (Voelker 2000).

We predict that a study of the nonbreeding ecology of Virginia's Warblers would establish one of the above possibilities (availability of late season resources within the breeding range, or winter territoriality) as the mechanism of the rapid molt we detected in this study. We conclude that there does not appear to be a single unifying pattern of molt migration or resource use among western-breeding passerine species; only if numerous species specific molt studies are conducted will we be able to determine whether few or many patterns exist with respect to molt and migration. This study and others highlight the potential loss of information inherent in time constraint models, if such models are themselves based on generalized observations of molt rather than on well-documented patterns within individual species. Finally, we contend that studies of wintering ecology, and the collection of data from nonbreeding specimens, are still desperately needed to aid in unraveling the interplay among different life history aspects of many common species.

ACKNOWLEDGMENTS

We thank the curators and staff at the following museums for loans: Canadian Museum of Nature (Ottawa), Denver Museum of Natural History, Museum of Comparative Zoology (Harvard Univ.), Natural History Museum of Los Angeles County, Museum of Natural Science (Louisiana State Univ.), Univ. of California Los Angeles Dickey Collection, American Museum of Natural History (New York), Cornell Univ. Ornithology Collection, Texas Coop. Wildlife Collection

(Texas A&M Univ.), Utah State Univ., Museum of Natural History (Univ. of Kansas), Bell Museum of Natural History (Univ. of Minnesota), Western Foundation of Vertebrate Zoology (Camarillo, California), San Diego Natural History Museum, Field Museum of Natural History (Chicago, Illinois), Univ. of Michigan Museum of Zoology, Museum of Vertebrate Zoology (Univ. of California, Berkeley), California Academy of Sciences (San Francisco), Moore Laboratory of Zoology (Occidental College), Univ. of Arizona, Delaware Museum of Natural History (Greenville), Smithsonian National Museum of Natural History (Washington, D.C.), and the Academy of Natural Sciences (Philadelphia). We also thank those curators without appropriate specimens that took the time to reply to our request. We thank two anonymous reviewers for helpful comments and criticisms.

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